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INTER-RELATIONSHIPS AND INHERITANCE OF AGRONOMIC AND
MORPHOLOGICAL CHARACTERS IN SPRING WHEAT

by



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A THESIS

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The undersigned certify that they have read and recommend to the Faculty of Graduate Studies for acceptance a thesis entitled "The Inheritance of Morphological and Agronomic Characters in Spring Wheat" submitted by Ping-hwa Hsu in partial fulfilment of the requirements for the degree of Master of Science.

ABSTRACT

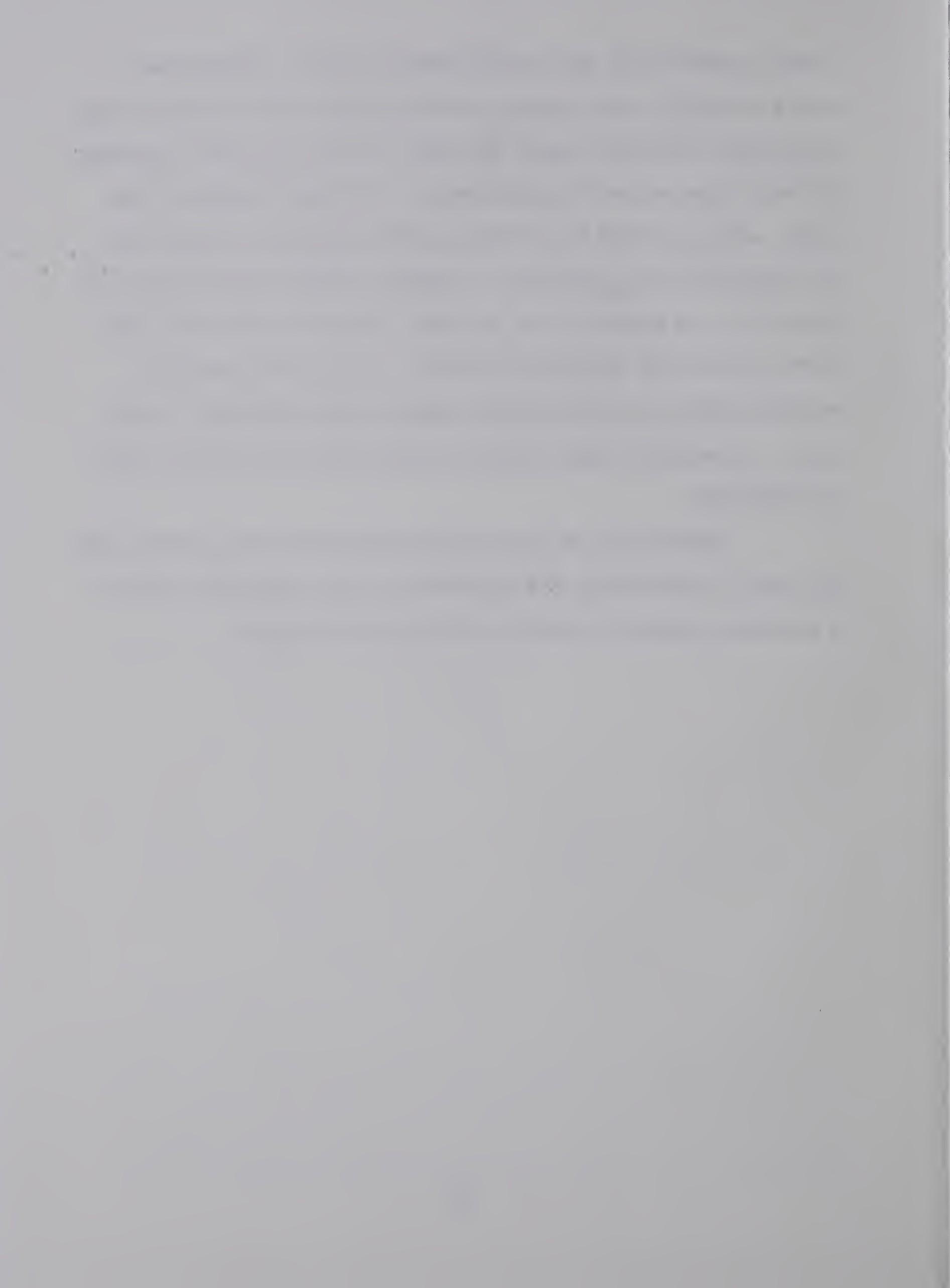
A complete diallel cross of five spring wheat varieties (Manitou, Pitic 62, Lerma Rojo 64A, Inia 66 and Wisconsin 261) was made. The parental varieties and F_1 progenies were compared in the greenhouse in 1968-69. Parental varieties, F_1 , F_2 and backcross progenies were evaluated again in the field in 1969. Simple correlation, partial correlation and regression, stepwise multiple regression and factor analysis were used to calculate and explore the relationships between yield, yield components and morphological characters. Diallel cross technique was employed to study the gene actions that controlled the inheritance of these characters.

The ear length, flag leaf sheath length, ear numbers per plant and spikelet numbers per ear in association made the largest contribution to the yield per plant, followed by a second group consisting of kernel numbers per ear, extrusion length and flag leaf breadth. Flag leaf length and 1,000-kernel weight formed a third group which also contributed substantially to the yield per plant. The effects of morphological characters on yield were found to be indirect, through their influences on yield components. The association of yield with its components and with morphological characters was affected by growth condition and the genotype-environmental interaction.

Evidence in this study suggested that a wheat plant with moderately short but broad flag leaf, long flag leaf sheath, short extrusion, long ear and moderately high tillering capacity would lead to increased yield per plant. As well as yield and its components, morphological characters under study appeared to be highly heritable and

largely controlled by genes having additive action. Dominance was more pronounced in the greenhouse condition than in the field for flag leaf length, extrusion length, the number of ears per plant, the number of kernels per ear and the yield per ear. Different degrees of dominance were also found in different growth conditions, and they were not significant in F_2 generation. Maternal effects were also more pronounced for the number of ears per plant, extrusion length and 1,000-kernel weight under greenhouse condition. In the field condition, maternal effects were observed for anthesis date and peduncle length only. For peduncle length, maternal effects were also evident in the F_2 generation.

Selection for an increased photosynthetic area above the flag leaf node in combination with selection for yield components would be a promising approach in breeding for high yielding wheat.



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TABLE OF CONTENTS

	Page
ABSTRACT	iii
ACKNOWLEDGEMENTS	v
LIST OF TABLES	vi
 CHAPTER	
I. INTRODUCTION	1
II. REVIEW OF LITERATURE	3
Growth Analysis and Plant Breeding	3
Statistical Genetics and Plant Breeding	8
Multivariate Statistical Analysis and Plant Breeding	14
III. MATERIALS AND METHODS	17
IV. RESULTS	27
Relationship Among Characters	27
Greenhouse Trial in 1968-69	27
Field Trial in 1969	33
Analysis of Variance for Diallel Table	37
Testing of Hypothesis	37
Greenhouse Trial, 1968-69	40
Field Trial in 1969	43
The F ₁ Diallel Table	43
The F ₂ Diallel Table	47
Non-allelic Interaction	47
Genotype-environmental Interaction	47
V. DISCUSSION	52
Relationships Between Yield, Yield Components, and Structures above the Flag Leaf Node	52
Inheritance of Yield, Yield Components, and Morphological Characters above the Flag Leaf Node	59
Conclusion	63
ANNOTATED BIBLIOGRAPHY	66

LIST OF TABLES

Table	Page
1. Correlation Coefficients Between Thirteen Characters of Five Parental Varieties and their F_1 Progenies	28
2. Partial Regression (b) and correlation (r) Coefficients Between Yield, Yield Components and Morphological Characters for Parents and F_1 Progenies from the Glasshouse Trial, 1968-69	29
3. Standardized Regression Coefficients from the Stepwise Multiple Regression Analysis for Yield per Plant from the Greenhouse Trial, 1968-69	31
4. Results of Factor Analysis for Parents and their F_1 Progenies from the Glasshouse Trial, 1968-69	32
5. Simple Correlation Coefficients Between Thirteen Characters of Five Parental Varieties and their F_1 , F_2 , Backcross Progenies	34
6. Partial Regression (b) and Correlation (r) Coefficients Between Yield, Yield Components and Morphological Characters for Parents, F_1 , F_2 and Backcross Progenies from a Field Trial, 1969	36
7. Standardized Regression Coefficients from the Stepwise Multiple Regression Analysis for Yield per Plant from the Field Trial, 1969	38
8. Results of Factor Analysis for Parents, F_1 , F_2 and Backcross Progenies from the Field Trial, 1969.	39
9. Mean Square Values from the Analysis of Variance for 5 x 5 Diallel Table (Greenhouse, 1968-69)	41
10. Components of Genetic Variation for 5 x 5 Diallel Crosses (Greenhouse, 1968-69)	42
11. Mean Square Values from the Analysis of Variance for 5 x 5 F_1 Diallel Tables (Field, 1969)	44
12. Components of genetic variation for 5 x 5 F_1 Diallel Cross (Field, 1969)	46
13. Mean Square Values from the Analysis of Variance for 5 x 5 F_2 Diallel Tables (Field, 1969)	48
14. Regression coefficients of W_r on V_r for 5 x 5 Diallel Tables in F_1 , F_2 and Backcross Generations	49

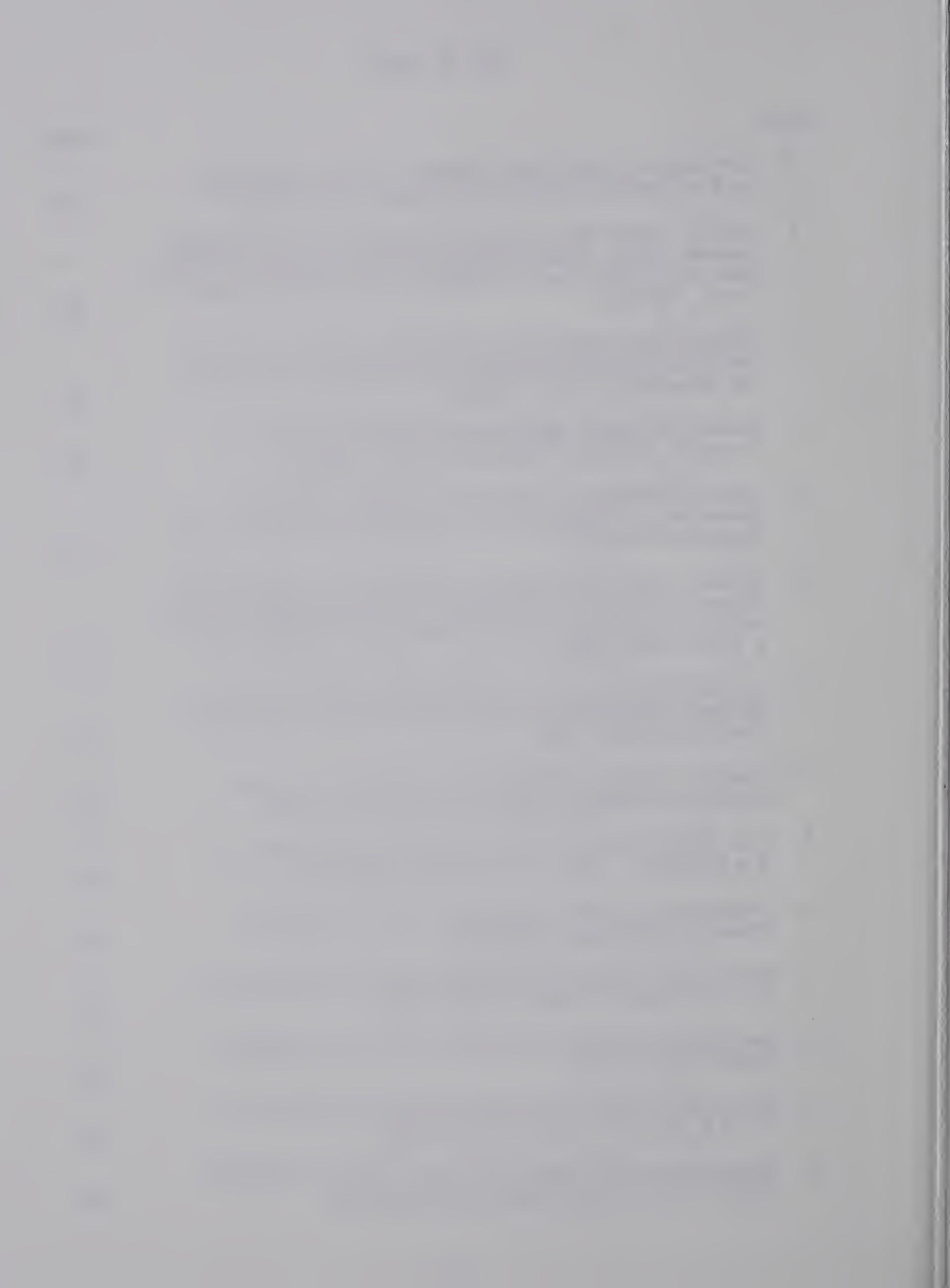


Table	Page
15. Mean Square Values from the Combined Analysis of Parental Performance over two Environmental Conditions	51
16. Mean Measurements of Yield and Yield Components for Parental Varieties in two Environmental Conditions	54

CHAPTER I

INTRODUCTION

The ever increasing demand for food, resulting from a fast expanding world population, can be met in two ways. Either the area of cultivated land may be increased or the level of yield per unit area may be raised. Since arable land is limited much of the emphasis must be placed on increasing crop yield. Wheat is one of the world's major foods. In this investigation, one method of increasing the yield of wheat by changing its genetic constitution will be considered.

With the rapidly expanding science of genetics and statistics, various breeding methods have been developed to apply our increased knowledge to the complicated quantitative inheritance of traits. Accordingly wheat breeding for high yield has moved from selection on the basis of yield performance to selection for yield components. However, improvement in yield has not occurred as frequently as was expected. Thus in recent years, turning from yield and its components, workers have drawn attention to physiological processes, and those morphological characters that contribute to the overall photosynthetic capacity. Among these morphological characters of the wheat plant, the photosynthetic area above the flag leaf node is the most important in relation to yield. Thus, there is available a new basis for selection which may lead to new and higher yielding wheat varieties.

Little has been reported on the inheritance of the morphological characters above the flag leaf node. Knowledge of the gene actions in control of these characters and the interrelationships among them can be useful to a plant breeder in planning his breeding program.

It is, thus, with the object of determining the nature of the inheritance of morphological structures above the flag leaf node and to determine if yield was associated with morphological characters in certain varieties that this study was undertaken.

CHAPTER II

REVIEW OF THE LITERATURE

Growth Analysis and Plant Breeding

One of the first attempts to analyze yield was made by Engledow and Wadham (1923) who partitioned the yield of cereals into its components. The number of plants per unit area, number of ears per plant, number of grains per ear, and weight per grain were regarded as the constituent parts that made up yield. Engledow and Wadham maintained that, following such analysis, it would be possible to "synthesize" high yielding forms. Selected strains were crossed to produce an optimum combination of yield components. This theory was later extended by various research workers. Smith (1936) devised a discriminant function for plant selection in terms of yield components. In winter wheat, Locke et al (1942) found a reasonably good association between yield and its components. Similar results were also reported by Krishnamurthy (1968), Fonseca and Patterson (1968), Tha and Ram (1969), Malik et al (1968), Johnson et al (1966), Smocek (1969), Jain et al (1969) and many others. Williams (1959) has shown that the use of components of yield could simplify the genetic description of this complex character. He also suggested that heterosis in the F_1 may result from independent additive gene action on two components of yield whose product contributed substantially to yield. Grafius (1964) approached the problem of breeding for yield on the basis of evaluating parents for pertinent yield components. He concluded that the prediction of yield of unselected, bulked, selfed progenies in self-pollinated crops would be related to the mid-parental value. Johnson

et al (1966) also pointed out that attention to expression of individual components of yield could provide a better basis for selection of parents and for evaluation of their progenies than yield itself.

However, such approaches have frequently been unsuccessful. Significant yield improvement has been achieved by selection for characters with relatively simple inheritance such as disease resistance. The production of plant types possessing good combinations of yield components has frequently proved difficult. It appeared that yield components were not independent. They were inversely correlated and circumstances that increase one tended to decrease another. Consequently, selection for high expression of one component, for example number of ears per plant, may imply selection for low expression of another such as number of grains per ear. Such cases were found to be very common in cereals. In studies with yield components in *Brassica campestris*, Ramanujam and Rai (1963) who used correlations and path coefficients to analyze the interrelation of six characters, came to the conclusion that it would be difficult to obtain a combination of yield components which gave a high yield. Thus, the use of the "components of yield" approach in plant breeding would be most effective if the components were highly heritable, if they were independent genetically, and if the characters were not associated physiologically (Mather, 1949; Fonseca and Patterson, 1968). However, the correlation of the genetical variation of yield components has been shown by Smith (1936) in Australian wheat. Physiological dependence was also implied by the wide array of compensating mechanism which contribute towards high yield (Donald, 1968). Therefore, the yield components approach is not the most effective way to reach maximum yield pro-

ductivity, although they are all highly heritable.

In an attempt to overcome such difficulties, Heath and Gregory (1938) drew attention to the value of growth analysis. Later, Watson (1952) pointed out that studies of yield components did not define yield-controlling characters useful to the plant breeders. Nelder (1963) also stated that yield components gave only an end pattern and could not say anything about the pathways by which the final yield was reached. Furthermore, they suggested a new approach to plant breeding for high yield through the study of physiological function as determined by growth analysis. Stoskopf et al (1963) supported this view and suggested that selection could be directed to the yield prerequisites which included all those factors which contributed to the overall photosynthetic capacity of the plant. Reasons for yield increases in modern barley and sugar beet varieties and the way in which they were related to growth pattern were demonstrated by Watson et al (1958, 1959). Problems in attaining maximum crop productivity were discussed by Loomis and Williams (1963). They concluded "The major limiting factors to total yield appears to be leaf area, its manner of display and CO₂ supply". Evidence of the importance of physiological functions have also been reviewed by Thorne (1966) who concluded that yield increases for cereals were closely related to photosynthetic area above the flag leaf node. Thus the flag leaf lamina, its sheath, and peduncle, are parts vital to yield. For spring wheat, Voldeng and Simpson (1967), and Simpson (1968) have presented evidence which supported these general conclusions. They too found high positive correlation between grain yield and the photosynthetic area above the flag leaf node. Smocek (1969) obtained the

association of flag leaf area with kernel number and average kernel weight, and the angle of the second leaf with ear number.

The relative importance of yield components in determining yield was reported by Jain et al (1968), Krishnamurthy (1968), Tha and Ram (1968), and Austenson and Walton (1970) in wheat. The contribution of different organs to the grain production of wheat have also been estimated quantitatively by removing the organs at ear emergence or by shading the stem or ear of wheat growing in the field, Boostra (1929) showed that ear contributed about 30%, and that the stems (including sheath) and leaves each contributed 25%, to the weight of grain produced. Almost all the leaf contribution came from the top two of the four green leaves. Smith (1933) showed by similar methods that the leaves and stem each contributed about 30% of the yield. The contribution to the yield by the ear was 41%. Other estimates of the ear contribution obtained by shading trials were, in pots, 48% (Thorne, 1962) and 25% (Quinlan and Sagar, 1962), and in the field, 26% (de Silva, 1961). Lower figures were reported by Rawson and Hofstra (1969). The same authors also found that throughout the development of wheat plant, there was movement of ^{14}C labelled photosynthate to all parts of the plant, the oldest leaf supplied the roots, and the flag leaf supplied the ear, intermediate leaves supplying the stem and tillers. The ear received assimilates almost exclusively from the flag leaf, 50% or more of the ^{14}C exported from the flag leaf being incorporated in the ear. Stored and remobilized material was transferred to the ear from other parts of the plant, but the amount was small. This evidence strongly supported the conclusions by Thorne (1966).

This appreciation of the importance of morphological struc-

tures introduced the plant breeders to a new method of selecting for high yield. This new approach to selection has been studied in winter wheat by Smocek (1968). He found that among the sixteen selection indices composed of various combinations of nine quantitative agronomic and morphological characters, maximum genetic gain was attained when flag leaf area was included in the combination of yield components. Thus there appeared to be good prospects for its use in the breeding of high yielding wheat. Such prospects would be greatly enhanced if information concerning the nature of the inheritance of these morphological characters were available. So far reports of this type of study have only been presented by Walton (1969) who analyzed a complete diallel cross of seven spring wheat varieties and concluded that flag leaf lamina area, extrusion of the head from the leaf sheath, head length, and yield were all controlled by polygenes. Additive gene action was shown to be an important genetic factor for all of these characters. Partial dominance played a part in the inheritance of yield, flag leaf area, and head length, over dominance was present for extrusion. Furthermore, Walton also showed that extrusion and flag leaf area were both positively correlated with yield.

Fundamentally, the ability to accept and transfer solar energy controls the yield (San Pietro et al 1967). Therefore, theoretically increasing photosynthetic area should increase yield. It often happened, however, that when modern intensive cultural practices such as heavy nitrogen application and close spacing were applied, yield was decreased by substantially increased photosynthetic area. This may be due to mutual shading of leaves, increased height, lodging and sterility. In order to overcome these difficulties, plant breeders

have attempted defining an ideal plant type. In rice, Jennings (1964), Jennings and Beachell (1964), and Jennings and Beachell (1967) have given details of a high yielding plant type with a high nitrogen response. This plant should be short, sturdy, with erect, thick, dark-green leaves. Early maturity moderate tillering capacity and insensitive to photoperiod were also considered to be important. Similarly, Donald (1968) suggested that for wheat a short, strong stemmed plant with few, small, erect leaves, a large erect ear with awn and a single culm was ideal.

Statistical Genetics and Plant Breeding

The difference between the discrete Mendelian mode of inheritance and the continuous type of inheritance was reconciled by Yule (1906) who suggested that there need not be any conflict between these two modes of inheritance if many genes having small and similar effects were postulated. Later in 1909, Johannsen showed that heritable and non-heritable agencies were jointly responsible for the variation in seed weight of beans, and that their effects were of the same order of magnitude and could be distinguished only by a breeding test. This established the concept of genotype and phenotype. In 1909, Nilsson-Ehle found that in wheat and oats there existed hereditary factors whose actions were similar, if not exactly the same. This provided evidence for the model of inheritance suggested by Yule (1906), and revealed that different genes could have similar and cumulative effects. The evidence which was the foundation of quantitative genetics was provided by East (1910, 1916) who studied the ear length of corn and corolla length of tobacco. Subsequently, Mather (1942), studied the

the abdominal chaetae number in *Drosophila melanogaster* and formulated the concept of the polygene. The essential features of polygene or multiple factor hypothesis were two; that the governing factors were inherited in the Mendelian fashion; and that they had effects similar to one another. The factors not only supplemented each other but had only small individual effects in comparison with the non-heritable variation.

In order to analyze and manage the continuous type of variation in quantitative inheritance, Fisher and Wright recognized the need to apply statistics and mathematics in such studies. In 1918, Fisher produced evidence of dominance of the polygenes and attempted the first partition of continuous genetic variation into components. Wright (1921) proposed the method of path coefficient which has solved a wide variety of inbreeding problems. Both of them partitioned the genotypic variance into three components; additive, dominant, and epistatic. This has since provided the foundation of the statistical approach to genetics.

Following the same approach proposed by Fisher et al (1932), the method to determine the components of variation from the cross of two inbred lines was developed by Mather (1949), and Mather and Vines (1952). Under the assumptions that there was no epistasis and that frequencies of alleles at each locus were 0.5 through all generations, Mather and Vines defined D as depending on differences between individuals distinguished by being homozygous for the two allelomorphs of the various genes, and H depends on the departure of the heterozygote from the mean of the two comparable homozygotes. Using a regression analysis, other methods have been developed by Cocherham (1954) and

Griffing (1950). Both of these methods were later combined in a generalized model by Anderson and Kempthorne (1954). All information about additive (D), dominance (H) and epistatic variation obtainable from the means of generations descended from two lines was contained in just six parameters. A study by Mather and Vines (1952) produced one of the most extensively used method. They were able to evaluate the relationship between genetic components and to determine the influence of epistasis, genotype-environmental interaction, and linkage.

The theory and usefulness of diallel techniques in genetic analysis of populations have received considerable attention in recent years. Several diallel cross methods have been proposed and applied to diverse problems. Diallel cross analyses differed in three main ways; in the material under investigation, in the postulates underlying genetic mechanism and in the methods of estimation. Three kinds of theory and analyses have been proposed. First was that by Jinks and Hayman (1953), Hayman (1954a, b, 1957, 1958, 1960) and Jinks (1954, 1955, 1956) who developed a diallel technique from the polygene theory and genetic notation of Mather (1949). They showed that it was possible to conduct an analysis of genetic variation and to make a graphical analysis of additive and non-additive variances. Since this method has many assumptions, complicated notations and was restricted to the nature of the material used, Dickinson and Jinks (1956) have generalized it, minimized the number of assumptions, and simplified its theory. The second method was that of Kempthorne (1956) and Matzinger and Kempthorne (1956) who emphasized the statistical analysis of the genetic model. Little practical use could be made of this technique for genetic and breeding studies. It is a method of mathematical

rather than biological interest. Third and last, Yates (1947) and Griffing (1956a and b) studied the diallel cross in terms of combining abilities. In plant breeding, this approach has contributed much in the selection of hybrid progenies and has helped to explain heterosis in genetic studies. (Sprague and Tatum, 1942; Henderson, 1952; Matzinger et al, 1959).

Among these three approaches, the one proposed by Jinks and Hayman has been the most extensively used. It was suited for self-pollinated crops, monocious, and self- and cross-compatible plants. When it is applied to self-incompatible or diocious plants, or animals, some modifications have to be made (Griffing, 1956a and b).

Most of the applications of diallel cross analysis have been limited to crops that could easily be crossed. For example, alfalfa (Theurer and Elling, 1963a and b; Wilcox and Wilsie, 1964), cotton (Marani, 1963; Miller and Marani, 1963; White and Richmond, 1963; White and Kohel, 1964), tobacco (Jinks, 1954; Hayman, 1954a and b), and even in barley (Upadhyaya and Rasmusson, 1967; Smith and Lambert, 1968; Eunus et al, 1962; Johnson and Aksel, 1959, 1964; Aksel and Johnson, 1961). The analysis of genotypic-environmental interaction by means of diallel cross was also studied by Allard (1956a).

In wheat, Krousted and Foote (1964) observed that a substantial part of genetic variation for yield, yield components and plant height was associated with general combining ability. Specific combining ability was large for grain yield and plant height. They concluded that diallel analysis for combining ability could be a promising technique for classifying parental lines of small grains in terms of

the hybrid performance, and for giving an understanding of the nature of quantitatively inherited traits. Crumpacker and Allard (1962) used the diallel cross analysis to evaluate heading date inheritance. In their study, ten varieties were crossed to form a complete diallel cross. Their analysis indicated that heritability was relatively high and partial dominance was predominant. Brown et al (1966) estimated the general and specific combining ability of the F_1 hybrids of three soft and four hard winter wheat varieties. They found that all genetic variance was ascribable to the general combining ability for grain weight, straw weight, number of spikes per plot, kernel weight, percent protein and plant height. No significant specific combining ability was found for any of these characters. Gyawali et al (1968) observed that both general and specific combining ability were responsible for the components of genetic variation in grain yield and its components. Whitehouse et al (1958) analyzed a diallel cross of four spring wheat varieties and found that the control of grain weight and number of grain per spikelet was mainly additive, and that an entirely additive genetic system controlled the number of spikelets per ear and number of ears per plant. However, the compound character, yield, showed non-allelic interaction which could be removed by logarithmic transformation. Lupton (1961), from the diallel analysis of six winter wheat varieties, observed that additive genetic effect controlled the expression of all of the characters studied. Complete dominance was significant for number of grains per ear, and for number of ears per plant while little dominance occurred for 1,000-kernel weight. Non-allelic interaction was again formed for yield but was removed by elimination of interacting varieties from the

analysis. In addition it was observed that the genetic system controlling yield reacted differently under various conditions, viz. different sowing methods, spacing and drilling.

The importance of the use of diallel cross analysis in a plant breeding program has been in the early identification of hybrids most likely to produce superior segregants. However, Gilbert (1958) criticized the diallel cross technique since its assumptions might not hold for the breeding material and that by mathematical manipulation, it was difficult to produce a clear-cut picture of the genetic system. Allard (1956b) evaluated the diallel analysis method in the genetic study of seed size in lima beans and concluded that with little effort the prepotency of the parents of 36 hybrids could be determined with useful accuracy. Johnson and Aksel (1959) and Johnson (1963) also supported this notion. They reasoned that the highest yielding arrays and crosses could be reliably determined by this technique. Moreover, this method could serve to detect the presence of significant non-allelic interactions attributable to complementary genes. In conclusion, Robinson (1963) stated that the usefulness of the method in the study of quantitative inheritance would probably depend upon the extent to which the results from diallel analysis could be generalized.

The inheritance of yield and its components, by means of methods other than diallel cross technique, were also reported. Anwar and Chowdhry (1969) crossed Pitic 62 with other three spring wheat varieties and found that earliness of heading was controlled by partial dominance, and yield per plant by overdominance. Since additive gene action was not important, the estimated heritabilities in narrow sense were low for them. Chapman (1967) found that heading date and plant

height were controlled by both additive and dominance gene action, but additive effects were greater than dominance effects. Tiller number was controlled by additive gene effects only while yield and seed size were conditioned by genes with dominance effects. Williams (1967) analyzed the generation means of yield and its components in a wheat cross and found that for yield, tiller number per plant, kernel number per ear, kernel weight and plant height, were inherited additively. Dominance was partial for tiller number and kernel weight. Additive or additive-dominance epistatic effects for yield, kernel number and tiller number were also shown.

Multivariate Statistical Analysis and Plant Breeding

Quantitative characters are greatly affected by environmental factors, and if a simply inherited character which is closely associated with a complex character such as yield can be found, selection for or against this complex character is greatly enhanced. In a breeding program, a plant breeder usually selects for several characters simultaneously. The relationships or relative importance among the traits selected are also important to him. In order to obtain this information, several statistical methods have been used.

The most commonly used statistical method in studying the relation between two characters when the cause-effect relationship is known involves the calculation of the correlation coefficient or regression coefficient. However the regression of dependent variables on a single independent variable alone is often inadequate to study the complex pattern when one result is the outcome of many causes. Then multiple regression and multiple correlation coefficient are used. The

partial correlation or regression coefficients in a multiple regression equation gives information about the relative contributions of the various independent variables to the dependent variable. However, there is no unique way of assessing the relative importance of the variables because the partial regression coefficients are greatly influenced by the sample standard deviations of independent variables. An easy and usually adequate way to learn the relative importance is to compare the magnitude of regression coefficients in the equation when the sample standard deviations are the same for all the independent variables. Thus, to avoid unequal variation in the independent variables, the standard partial regression coefficients may be calculated and compared. Furthermore, to ensure that only important independent variables are in the resulting multiple regression equation, the step-wise multiple regression method was recently postulated by Efroymson (1962), and Draper and Smith (1967). This method is so devised that an equation is obtained by adding one independent variable at a time according to its relative importance in determining the dependent variable.

The use of partial correlation, partial regression, multiple correlation and multiple regression methods required that certain roles be assigned to some of the causes. For a partial correlation analysis it was necessary to decide which variables were to be correlated and which of the remaining causes must be held constant. Multiple correlation requires that one cause be dependent upon some or all of the remaining variables. All these choices depend upon the nature of the causes and on information other than the values of their correlations. The conclusions that could be drawn about the dependence structure would

in turn depend upon those choices. Furthermore, if the analyses were repeated for different choices of the dependent or constant variates, the successive findings would not be independent or contain mutually exclusive information about the structure. The above considerations apply equally to the path coefficient analysis because it was the same as standardized partial correlation analysis. Factor analysis, on the other hand, could analyze the dependence structure and determine the factors which have generated the dependence or variation in the responses.

Factor analysis has been described as "a statistical technique for reducing a large number of correlated variables to terms of a small number of uncorrelated variables. The correlated variables consist usually of measurements for observable traits; the uncorrelated variables, called factors, are abstract hypothetical components" (Burt and Banks, 1947). Originally, this method was devised for studies in psychology. Because of its power to elicit the underlying multivariate structure, it has been used in biological research, especially in numerical taxonomy (Seal, 1966). In the present study, an attempt was made to apply it to the study of relationships between yield and agronomic and morphological characters. In order to study the relative contribution of each factor to yield, it was assumed that the agronomic and morphological characters studied accounted for all of the variation in yield and this could be determined by the multiple correlation coefficient between them.

CHAPTER III

MATERIALS AND METHODS

A Canadian commercial variety, Manitou, was crossed with three varieties of Mexican origin (Pitic 62, Lerma Rojo 64A and Inia 66) and Wisconsin 261, an American variety. The crosses, between these five varieties, were made in all possible combinations to form a diallel cross. Such an arrangement for n parental varieties yields $n(n-1)$ crosses reciprocals included. Comparisons were thus made among a total of 25 families, including the parental varieties. The hybrid material was provided by Dr. P.D. Walton, by whom the crosses were made in the summer of 1968. The F_1 and the parental varieties were compared in the green-house during the winter of 1968-69 using a randomized complete block design with two replications. Each single plot consisting of 2 plants was planted at a spacing of 12.7 cm between plants and 15.2 cm between rows on October 10, 1968.

The date of anthesis was recorded for each plant. At maturity, flag leaf length, flag leaf breadth, flag leaf sheath length, extrusion of the head from the leaf sheath and ear length were measured. The number of ears per plant and the number of kernels per ear, as well as spikelets per ear, in the main tiller were counted. The seed produced by each plant was weighed and counted and, from these data, the 1,000-kernel weights were calculated. The length of peduncle was also calculated from the length of extrusion and sheath. A set of backcrosses of the F_1 hybrid to each parental variety was made in the green-house in the winter of 1968.

The 20 F_1 families, 20 F_2 families, and 20 backcross families,

together with 3 sets of parental varieties and 6 fillers were grown in a 9 x 9 repeated simple lattice design trial in the field with 4 replications. Each plot, consisting of one row of 5 seeds randomly chosen from each family, was sown at a 30.48 x 30.48 cm spacing on May 14, 1969. This experiment was located on unirrigated land at the University of Saskatchewan. All characters studied in the greenhouse were measured in the field by the same method.

The data pertaining to these characters were analyzed by using the standard technique for a repeated simple lattice design outlined by Cochran and Cox (1957). The adjusted line mean values for each character in each generation were used for the genetic analysis by means of the methods developed by Hayman (1954), Jinks (1954, 1956) and Griffing (1956).

The correction of line effect, proposed by Yates (1936), in a repeated simple lattice design was that the corrected line effect was no longer confounded with block effect and that it was equalized on a level with other lines. The line effect therefore could be assumed to be of a pure genotypic nature. This could also be seen from the mathematical models:

The corrected line effect could be represented as

$$T_{ij} = U_{ij} + \bar{B}_{..} + S(E.T)$$

while the content of mean line effect over blocks was

$$\frac{T_{ij}}{2r} = U_{ij} + \bar{B}_{i.} + \bar{B}_{.j} + S(E.T)$$

Where U_{ij} was the line genotypic value, $\bar{B}_{i.}$ was the total block effect in r replications of X groups, $\bar{B}_{.j}$ was the total block effect in r

replications of Y groups and S(E.T) was the respective error term. The corrected line effect from the first equation was equalized on a level of $\bar{B}_{..}$, the grand mean of block effects, but the uncorrected mean value over blocks was confounded with either \bar{B}_i . or \bar{B}_j the block effects in X and Y group respectively. Therefore, when these corrected line mean values were used for the genetic analysis they could be considered as pure genotypic value.

Since the adjusted line mean values were used for the genetic analysis, E, the environmental error was estimated from the reciprocal differences in each diallel table. A factor 1/2 was used as multiplier compensate for the replacement of each pair of measurements of reciprocals by their common mean. These estimates and adjustments were in accordance to Hayman's (1954a) hypotheses. For the same reasons, the t-test suggested by Hayman (1954b) was used to test the validity of the diallel analyses hypotheses.

Simple correlation coefficients, partial correlation coefficients and partial regression coefficients between yields, yield components, and morphological characters were calculated from both mean values over blocks for greenhouse trial and adjusted mean values for field trial. All correlation analyses and regression analyses were calculated and tested by the standard as set up by Snedecor (1946). In order to compare the relative importance of yield components and morphological characters, the stepwise multiple regression method formulated by Draper and Smith (1967) was employed.

To study the dependence structures of the characters observed in two environments, the correlation matrix was subjected to factor analysis. The method and interpretation of factor analysis was that

explained by Lawley and Maxwell (1963) and Harman (1960).

Since in the biological and behavioral sciences, a great many phenomena are multiply determined and independent variables are not easily located, the application of factor analysis may be used to disentangling such interrelationships among the variables. Such an analysis has two objectives; first to reduce the number of variables by combining those which are most closely related, and second to transform such groups into independent variables.

The basic assumptions of factor analysis are that a set of observed correlated variables x_i can be accounted for in terms of a smaller set of hypothetical variables or common factors f_r and a set of independent residual variables e_i . Also it is assumed that x_i form a multivariate normal distribution, and that the f_r are orthogonal. If C is the variance-covariance matrix of p variables which constitute x_i , L is the matrix of loadings of f_r , and V is the diagonal matrix of the residual variables e_i , then the basic model of factor analysis is $C = LL' + V$. The object is to find a set of consistent and efficient estimates of element parameters in L and V , or mathematically, to analyze the matrix L for its latent roots and vectors. When x_i are standardized, the matrix C is a matrix of correlations. The computation is thus started from the correlation matrix C which is experimentally obtained. Since the correlation of each test with itself would give diagonal values of unity which would be without meaning, these values are replaced by communalities. The communalities are the amount of the variance of the variable accounted for by the common factors together. In most cases, this will be less than the whole variance, so it will leave a residue to be accounted for. Because of the nature

of the model, the choice of the communality values and the determination of the number of factors have been the most difficult problems in this analysis. Lawley (1940) and Rao (1952) suggested the maximum likelihood method. Here a solution is obtained by iteration which evolves going to and from between communalities and the number of factors until a combination which yields the smallest residual value is obtained. Cattell (1965) proposed to fix the number of factors and then find, by iteration, communalities that exactly fit the off-diagonal to give that number of factors. In the present study, the communalities were fixed by taking the highest correlation in each row or column of the C matrix and using these as the approximate values of the loadings. Iteration continues until the values converge at the best approximation. The loadings of the first or the most important factor having been found, its effect on L is removed and the process is repeated on the residual matrix in order to find further factors. This procedure results in factors being arranged in order of increasing triviality. When the contribution of a factor to the total variance was less than 10%, the process is stopped. Thus the important factors are retained; the trivial factors are discarded. This was the method set out by Harman (1960). Due to the nature of the model, the maximum likelihood method leads to equations for estimating the elements of matrix L which are satisfied by an infinity of solutions, all equally good from the statistical point of view. Therefore, this property allows any orthogonal rotation of the primary result in anyway the experimenters find desirable. Several approaches to rotation in factor analysis have been proposed. However, the varimax rotation method suggested by Kaiser (1958) was used here.

The resultant factors are mutually orthogonal and in this connection the loadings are also the weights to be given to the factors in regression equations which estimate the contribution of the variables. The squares of the loadings of a given factor totalled over the given set of variables indicates the magnitude of its contribution to the variables as a whole. In other words, it gives the percentages of the factors contributing to the total variance. Furthermore, the factors reproduce the correlations between variables exactly. Thus, following these properties, factor analysis indicates both groupings and percentages contribution.

Diallel crossing techniques may vary with inclusion or exclusion of parental inbreds, reciprocal F_1 's, and with sampling assumptions. Griffing (1956b) presented four possible cases of diallel cross methods:

- (1) parents, F_1 's and reciprocals included: n^2 combinations;
- (2) parents and one set of F_1 's included: $[1/2n(n+1)]$ combinations;
- (3) one set of F_1 's and reciprocals, the parents excluded: $n(n-1)$ combinations;
- (4) F_1 's only, both reciprocals and parents excluded: $1/2n(n-1)$ combinations.

These four cases and two sampling assumptions (random and fixed populations) give rise to eight different situations, each requiring a different analysis. Suitable methods have been set out by Griffing (1956b) to determine combining abilities.

The Hayman-Jinks analysis of diallel tables formed from parent and F_1 data assumes that:

- (1) the parents are homozygous,
- (2) there is no epistasis,
- (3) there is no multiple allelism,
- (4) there is no difference between reciprocal crosses,
- (5) diploid segregation,
- (6) the genes are independently distributed between parents,
- (7) there are no genotype interactions with locations and years.

Using this method, components of variation for diallel crosses may be calculated.

The components of variation which were evaluated by Jinks and Hayman (1953) are:

$$D = \sum 4u_i v_i d_i^2$$

$$H_1 = \sum 4u_i v_i h_i^2$$

$$H_2 = \sum 16u_i^2 v_i^2 h_i^2$$

$$F = \sum 8u_i v_i (u_i - v_i) d_i h_i$$

$$h = \sum 4u_i v_i h_i$$

In these formulae, d_i is half the difference between the homozygotes while h_i is the difference between the heterozygote and the mid-parent (mean of the two homozygotes). The ratio of number of positive and negative homozygotes in the parents is taken as $u_i : v_i$ where $u_i + v_i = 1$.

H_1/D measured the average degree of dominance over all loci and $(H_1/D)^{1/2}$ was a weighted estimated degree of dominance. $H_2/4H_1$ pro-

vided an estimate of the mean value of $u_i v_i$ which indicated the proportion of positive and negative alleles in the parents and had a maximum value of 1/4 when $u_i = v_i = 1/2$. An estimate of the relative frequencies of dominant and recessive alleles is shown by F which is positive if there is an excess of dominant alleles.

Following the same approach, Hayman (1954b) has also defined the variance of parents (V_p), the covariance between the parents and their offsprings in the rth array (W_r), the variance of the rth array (V_r), the means of offspring variances (V_m), and the mean covariance between the parents and the offsprings (W_m) as follows:

$$V_p = D + E$$

$$W_r = 1/2D - 1/4F_r + E/n$$

$$V_r = 1/4D + 1/4H_1 - 1/4F_r + \frac{n-1}{2n} E$$

$$V_m = 1/4D + 1/4H_1 - 1/4H_2 - 1/4F + \frac{1}{2n} E$$

$$W_m = 1/2D - 1/4F + E/n$$

$$V_r = 1/4D - 1/4F + 1/4H_1 - 1/4H_2 + \frac{1}{2n} E$$

Where n is the number of parents, and E is the environmental component of variation.

From the above three statistics, V_r , W_r and V_p a graphic analysis was possible (Hayman, 1954b), and important information could be obtained. When there was no dominance the regression line of W_r on V_r is tangent to the limiting parabola $W_r^2 = V_p V_r$. The regression line shifts to the right as the degree of dominance over all loci

increases. Furthermore, positions along the regression line indicate the dominance order of the parents.

A consequence of hypotheses on which these analyses were based was that $W_r - V_r$ was constant (i.e. independent of the array) if the hypotheses were valid. A significance test could be made with an analysis of variance over the line and block differences, and a significant line effect would indicate failure of the hypotheses. If the adjusted mean values were used for these analyses, a t-test of the following formula given by Hayman (1954b) would be used:

$$t^2 = \frac{(n-2) (Var. V_2 - Var. W_r)^2}{4 Var. V_r \times Var. W_r - Cov.^2 (V_r, W_r)}$$

The t value was tested with $n-2$ degrees of freedom.

The analysis of variance of a diallel table proposed by Hayman (1954a) included parents and both sets of F_1 crosses. The appropriate sampling assumption was that the experimental material itself represented the entire population about which inferences were to be made. Hence, with respect to Griffing's classification of diallel crossing techniques, it was applicable to experimental method 1 with a fixed model.

This analysis of variance divided variation into four parts :

- (a) the variation in the mean effect of each parental line;
- (b) the variation in the reciprocal sums not ascribable to (a);
- (c) the average maternal effects of each parental line;
- (d) the variation in the reciprocal differences not ascribable to (c).

This linear model was further extended by partitioning (b) into three components:

- (b₁) was the mean dominance deviation;
- (b₂) was the further dominance deviation due to the rth parent;
- (b₃) was the remaining discrepancy in the rsth reciprocal sum.

In a comparison of the analysis of variance methods proposed by Hayman (1954a) and Griffing (1956b), it was observed that (a) was equivalent to the general combining ability, (b) was equal to the specific combining ability, and the pooled (c) and (d) was equal to the reciprocal effects. This comparison was made for method 1 with fixed model and when the mean values of each family were used for analysis.

CHAPTER IV

RESULTS

Relationship Among Characters

Greenhouse Trial in 1968-69

Simple correlation coefficients between characters calculated from the data recorded for parental varieties and their F_1 progenies were presented in Table 1. Of the structures above the flag leaf node, the ear length, flag leaf breadth and sheath length were closely associated with yield per plant. Correlations between anthesis date and other characters indicated that late flowering lines had shorter flag leaves and more spikelets per ear. Fewer kernels were developed when flowering was late but the kernel size, measured by 1,000-kernel weight, was larger than in early flowering lines. Lines with long flag leaves also tended to produce broad flag leaves, while long peduncle and greater extrusion were closely associated with each other and also with long flag leaves. Increases in flag leaf breadth, on the other hand, were associated with increases in sheath length and in the number of ears per plant. Increased sheath length was associated with increased peduncle length. Long peduncle and greater extrusion were both accompanied by a reduction in 1,000-kernel weight and thereby reduced the yield per ear. All yield components were closely associated with yield per plant, while only the number of spikelets per ear and the number of kernels per ear were associated with yield per ear.

Partial correlation and regression coefficients for all observed characters were also calculated and presented in Table 2. There

Table 1

CORRELATION COEFFICIENTS BETWEEN THIRTEEN CHARACTERS OF FIVE PARENTAL VARIETIES AND THEIR F_1 PROGENIES

	Flag leaf length	Flag leaf breadth	Peduncle length	Extrusion	Ear number per plant	Spikelet number per ear	Kernel number per ear	1,000 kernel weight	Yield per ear	Yield per plant
Anthesis date	-0.46**	n.s.	n.s.	n.s.	n.s.	0.49**	-0.49**	0.42**	n.s.	n.s.
Flag leaf length	0.31*	0.39	0.41*	0.41*	n.s.	n.s.	-0.40	*0.42*	n.s.	n.s.
Flag leaf breadth	n.s.	n.s.	0.28*	n.s.	0.42	n.s.	n.s.	n.s.	n.s.	0.43**
Peduncle length	0.94**	0.37*	n.s.	n.s.	n.s.	n.s.	-0.43	-0.29*	*	n.s.
Extrusion length	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	-0.40	-0.29*	*	n.s.
Sheath length	0.56**	0.67*	0.61*	0.61*	n.s.	n.s.	n.s.	n.s.	0.61**	
Ear length	0.34*	0.64*	0.60	0.60	n.s.	n.s.	0.39	0.38	**	
Ear No. per plant	0.61*	0.31*	n.s.	n.s.	n.s.	n.s.	0.87	0.87	**	
Spikelet No. per ear	n.s.	n.s.	n.s.	n.s.	0.28*	0.28*	n.s.	0.35	**	
Kernel No. per ear	-0.37*	0.49	0.49	0.49	n.s.	n.s.	0.58	0.58	**	
1,000 kernel wt.	n.s.	0.30	n.s.	n.s.	n.s.	0.35	0.35	0.35	0.35	
Yield per ear										0.35

*** - significant at 0.1%
 ** - significant at 1%
 * - significant at 5%
 n.s. - not significant

Table 2

PARTIAL REGRESSION (b) AND CORRELATION (r) COEFFICIENTS BETWEEN YIELD, YIELD COMPONENTS AND MORPHOLOGICAL CHARACTERS FOR PARENTS AND F₁ PROGENIES FROM THE GLASSHOUSE TRIAL, 1968-69

	Components of yield						Morphological characters						Multiple correlation coefficient
	Ear No.	Yield per plant	Spikelet number per ear	Kernel weight per ear	1,000 kernel number	Ear length per ear	Extrusion length	Sheath length	Flag leaf length	Flag leaf breadth	Flag leaf width	Flag leaf area	
Y	b	6.073**	1.625*	-0.133	-0.156	0.002	0.567*	-0.065	3.652*	0.694*	0.895	0.895	
	r	0.824	0.343	-0.037	-0.107	0.095	0.019	-0.211	0.357	0.727	0.727	0.727	
Yield per plant	b						-0.019	-0.007	0.102*	-0.002	0.361	0.646	
	r						-0.094	-0.145	0.609	-0.054	0.269	0.646	
Ear No. per plant	b						0.140	-0.004	-0.072*	-0.016*	0.484*	0.660	
	r						0.531	-0.071	-0.439	-0.332	0.323	0.660	
Yield per ear	b						0.090*	0.006	0.078	-0.030*	0.314	0.808	
	r						0.394	0.128	0.491	-0.577	0.229	0.808	
Spikelet No. per ear	b						0.542*	-0.029	-0.110	0.042*	0.101	0.681*	
	r						0.626	-0.181	-0.241	0.292	0.023	0.681*	
Kernel No. per ear	b						-1.119	-0.338	-0.135	-0.339	1.645	0.526*	
	r						-0.189	-0.241	-0.036	-0.278	0.045	0.526*	
1,000 kernel weight	b												
	r												

** - significant at 0.1%
 * - significant at 1%
 * - significant at 5%

was evidence that the number of ears per plant and yield per ear, in that order, made the largest contributions to yield per plant. The number of spikelets per ear was the character most closely associated with the ear number per plant, while kernel number per ear and 1,000-kernel weight were associated with yield per ear. Of the morphological characters considered the length of flag leaf sheath and the breadth of the flag leaf were the characters which led to high yield per plant. Sheath length was also important in increasing spikelet number but it reduced yield per ear. Flag leaf length together with sheath and ear length were associated with the number of spikelets per ear. All morphological characters studied, except extrusion, sheath and the ear length and flag leaf breadth were positively and significantly associated with yield per ear. The multiple correlation coefficients showed that the components of yield accounted for 90% of the variation in yield per plant while morphological characters accounted for about 70%.

The result of stepwise multiple regression analysis (Table 3) showed that the standardized regression coefficient was significant for ear number per plant only. Except for kernel number per ear, the trend indicated that yield components were more important than the morphological characters in predicting yield per plant. Of the 89.5% of the variation in yield which were predictable by both yield components and morphological characters, 87.2% was accounted for by the number of ears per plant alone. Other characters showed no significant relationship.

The results of the factor analysis which included rotation by the varimax method, were presented in Table 4. Since there was in-

Table 3

STANDARDIZED REGRESSION COEFFICIENTS FROM THE STEPWISE MULTIPLE REGRESSION
ANALYSIS FOR YIELD PER PLANT FROM THE GREENHOUSE TRIAL, 1968-69

Ear No. per plant	1,000 kernel weight	Ear length	Leaf breadth	Leaf length	Extrusion number per ear	Spikellet number per ear	Kernel number per ear	Sheath length	Multiple correlation coefficient
0.872**									0.872
0.879**	0.087								0.876
0.842**	0.108	0.113							0.882
0.814**	0.108	0.104			0.074				0.885
0.801**	0.072	0.094			0.106	0.084			0.888
0.807**	0.095	0.087			0.143	-0.127	0.099		0.891
0.876**	0.121	0.148			0.153	-0.190	0.129	-0.140	0.894
0.867**	0.133	0.116			0.155	-0.197	0.141	-0.131	0.895
0.848**	0.137	0.099			0.156	-0.203	0.140	-0.138	0.037
									0.895

** - significant at 0.1%

Table 4

RESULTS OF FACTOR ANALYSIS FOR PARENTS AND THEIR F_1
PROGENIES FROM THE GLASSHOUSE TRIAL, 1968-69

Characters	Communalities	Factor 1	Factor 2	Factor 3
Spikelet No. per ear	0.866	0.885	-0.283	-0.042
Kernel No. per ear	0.500	0.391	0.366	0.461
1,000-kernel weight	0.661	-0.116	-0.799	-0.095
Ear length	0.672	0.763	0.238	0.183
Extrusion length	0.749	-0.014	0.764	-0.407
Sheath length	0.699	0.817	0.103	0.144
Flag leaf length	0.782	-0.257	0.702	0.473
Flag leaf breadth	0.791	0.155	-0.055	0.874
Ear No. per plant	0.664	0.701	-0.098	0.404
Percentage	63.86%	27.82%	20.09%	15.94%

determinacy in the estimates of the factor parameters, the resulting factors can be interpreted in a meaningful way by looking at the higher loadings only. Factor 1 consisted of ear numbers per plant and spikelet number per ear closely associated with the length of ear and sheath. For factor 2 the largest loading was for 1,000-kernel weight. This character was negatively associated with flag leaf length and extrusion and, after the effect of factor 1 had been removed, was the second most important. The third factor was kernel number per ear together with large contribution from flag leaf breadth and smaller contribution from flag leaf length and extrusion. The results in Table 4 show that 27.82% of the total variation in yield could be explained by the first factor; 20.09% and 15.94% by the second and third factors. Thus a total of 63.86% of the variation in yield were accounted for by these three factors.

Field Trial in 1969

Correlation coefficients were calculated between thirteen characters using data from five parental varieties, their first and second generation progenies and their backcross progenies (Table 5). All the components of yield were closely correlated with yield per plant with the exception of 1,000-kernel weight. Of the morphological structures above the flag leaf node, peduncle length and the flag leaf length were not associated with yield per plant. Flag leaf breadth, both sheath and ear length, however, were closely and positively correlated with yield per plant. Lines in which anthesis was late gave high yield. Late flowering lines also had more ears, more spikelets and more kernels but with a lower kernel weight.

Table 5

SIMPLE CORRELATION COEFFICIENTS BETWEEN THIRTEEN CHARACTERS OF FIVE PARENTAL VARIETIES
AND THEIR F_1 , F_2 BACKCROSS PROGENIES

	Flag leaf length	Flag leaf breadth	Peduncle length	Extrusion	Ear number per plant	Spikelet number per ear	Kernel weight per ear	Yield per ear	Yield per plant
Anthesis date	-0.32*	0.33**	n.s.	n.s.	0.57**	0.44**	0.47**	0.29*	-0.40**
Flag leaf length	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.36	n.s.	0.38***
Flag leaf breadth	n.s.	n.s.	0.54	0.54**	0.46	0.59**	0.54	n.s.	0.47**
Peduncle length	n.s.	n.s.	0.97	0.51	-0.31*	0.25*	n.s.	-0.39	n.s.
Extrusion	n.s.	n.s.	0.29**	-0.50	n.s.	-0.34**	-0.52	n.s.	-0.42**
Spikelet length	n.s.	n.s.	0.54	0.65	0.55**	0.55	0.29*	n.s.	0.57***
Ear length	n.s.	n.s.	0.42	0.77	0.69	0.69	n.s.	0.59	0.72***
Ear No. per plant	n.s.	n.s.	0.53	0.25*	0.25*	0.25*	-0.39	n.s.	0.74***
Spikelet No. per ear	n.s.	n.s.	0.63	n.s.	n.s.	0.49*	n.s.	0.73***	n.s.
Kernel No. per ear	n.s.	n.s.	0.31	n.s.	n.s.	0.92*	0.79***	n.s.	n.s.
Yield per ear	n.s.	n.s.	0.71	n.s.	n.s.	n.s.	n.s.	n.s.	0.71***

*** - significant at 0.1%
** - significant at 1%
* - significant at 5%
n.s. - not significant

Morphological structures above the flag leaf node were also related to yield components. Extrusion was negatively correlated with yield per plant. The flag leaf breadth, leaf sheath and the ear length were positively correlated with spikelets and kernels per ear. Greater extrusion was associated with fewer spikelets and kernels per head. Greater ear length, broader flag leaves, shorter peduncles and shorter extrusions were associated with increased yield per ear. Changes in flag leaf length were correlated only with changes in 1,000-kernel weight. The late flowering lines which gave higher yields also had longer sheaths, longer ears, and broader but shorter flag leaves. Higher ear numbers were accompanied by longer peduncles, sheaths, ears and broader leaves.

The partial correlation and partial regression coefficients (Table 6) indicated that plant yield was associated with all its components. Among them, ear number, kernel number and 1,000-kernel weight were the most important. Higher ear number was accompanied by larger spikelet number but fewer kernels. The yield per ear was found to be directly correlated with kernel number and 1,000-kernel weight.

Of the morphological characters, the two associated with yield per plant were sheath length and flag leaf breadth. Sheath length associated with the number of ears per plant and yield per plant, while flag leaf breadth was linked with yield per ear. The number of kernels per ear increased with greater ear length and broader flag leaves and decreased with longer extrusion. The 1,000-kernel weight was increased with longer flag leaves. The multiple correlation coefficients showed that the components of yield accounted for 99% of the variation in the yield per plant. The morphological structures

Table 6

PARTIAL REGRESSION (b) AND CORRELATION (r) COEFFICIENTS BETWEEN YIELD, YIELD COMPONENTS AND MORPHOLOGICAL CHARACTERS FOR PARENTS, F_1 , F_2 AND BACKCROSS PROGENIES FROM A FIELD TRIAL, 1969

γ	Components of yield					Morphological characters					Multiple correlation coefficient
	Ear No. per plant	Yield per ear	Spikelet number per ear	Kernel number per ear	1,000 kernel weight	Ear length	Extrusion length	Sheath length	Flag length	Flag leaf breadth	
Yield per plant	b r	1.233 0.970	0.349*	0.210*	0.045*	0.521*					0.992
Ear No. per plant	b r		0.255	0.270	0.624	0.685					
Yield per ear	b r			1.106**	-0.005	-0.419**					0.615*
				0.460	-0.088	-0.349					
				-0.125*	0.041**	0.317					
				-0.246	0.954	0.774					
Yield per plant	b r						2.244	-0.282	1.543*	2.066*	*
Ear No. per plant	b r						0.164	0.160	0.242	0.295	0.791
Yield per ear	b r						0.162	0.008	1.325**	-0.382	0.708
Spikelet No. per ear	b r						0.026	0.073	0.311	-0.158	0.160
Kernel No. per ear	b r						1.057	-0.195	-0.088	0.366	0.819*
1,000 kernel weight	b r						0.221	-0.222	-0.029	0.200	0.242
							0.868**	-0.064	0.322	0.056	0.368
							0.335	-0.141	0.198	0.060	0.228
							2.843*	-0.444*	0.170	0.518	2.027*
							0.272	-0.234	0.026	0.133	0.274
							0.416	-0.034	-0.339	0.800**	-0.309
							0.077	-0.034	0.095	0.358	0.080
											0.431*

*** - significant at 0.1%
 ** - significant at 1%
 * - significant at 5%

above the flag leaf node accounted for nearly 80%.

The result of stepwise multiple regression analysis (Table 7) indicated that the standardized regression coefficients were significant for the three primary yield components. Almost all of the variation in yield per plant was predictable by ear number per plant, kernel number per ear and 1,000-kernel weight. Other characters were not significant. It was also shown that the importance of yield components in determining yield per plant were more direct than were morphological characters.

The result of factor analysis, after varimax rotation, was presented in Table 8. It was indicated that 70% of the variation in yield per plant were explainable by the resulting three factors. Among them, 27.68% was contributed by ear number and spikelet number closely associated with sheath length, flag leaf breadth and ear length (factor 1). After removing the effect of factor 1, factor 2 could be regarded as a factor of kernel number, which was associated with spikelet number, extrusion and ear length. This factor accounted for 26.97% of the variation in yield. The remaining 14.72% was due to the combination of 1,000-kernel weight and flag leaf length which formed the factor 3.

Analysis of Variance for Diallel Table

Testing of Hypothesis

Using the formula of t-test given by Hayman (1954b), the validity of the hypotheses, on which the diallel analysis was based, were tested. Since none of them was significant at 5% level, the basic assumptions underlying the diallel cross analysis were valid.

Table 7
STANDARDIZED REGRESSION COEFFICIENTS FROM THE STEPWISE MULTIPLE
REGRESSION ANALYSIS FOR YIELD PER PLANT FROM THE FIELD TRIAL, 1969

Ear No.	Kernel number per plant	1,000 kernel weight per ear	Spikellet number per ear	Flag leaf length	Flag leaf breadth	Extrusion	Ear length	Sheath length	Multiple correlation coefficient
0.736**	0.578***	0.644***	0.616***	0.245***	0.245***	0.044	0.044	-0.027	0.736
0.679***	0.661***	0.593***	0.593***	0.245***	0.254***	0.039	-0.030	0.020	0.965
0.661***	0.660***	0.586***	0.586***	0.254***	0.254***	0.041	-0.032	0.020	0.990
0.655***	0.653***	0.589***	0.589***	0.255***	0.255***	0.043	-0.032	0.20	0.991
0.653***	0.653***	0.590***	0.590***	0.255***	0.255***	0.042	-0.031	0.019	0.991
0.653***	0.653***	0.590***	0.590***	0.255***	0.255***	0.042	-0.031	0.003	0.991

*** - significant at 0.1%

Table 8

RESULTS OF FACTOR ANALYSIS FOR PARENTS, F_1 , F_2
AND BACKCROSS PROGENIES FROM THE FIELD TRIAL, 1969

Characters	Communalities	Factor 1	Factor 2	Factor 3
Spikelet No. per ear	0.785	0.599	0.648	-0.078
Kernel No. per ear	0.756	0.291	0.815	0.086
1,000-kernel weight	0.662	-0.285	0.133	0.751
Ear length	0.832	0.468	0.780	-0.066
Extrusion length	0.902	0.358	-0.873	0.109
Sheath length	0.833	0.906	0.053	-0.101
Flag leaf length	0.768	0.093	-0.151	0.858
Flag leaf breadth	0.670	0.674	0.439	0.152
Ear No. per plant	0.731	0.783	0.089	-0.331
Percentage	69.38%	27.68%	26.97%	14.72%

Greenhouse Trial, 1968-69

The mean square values (Table 9) for (c) were significant for anthesis date, extrusion of the head above the flag leaf, peduncle length, number of ears per plant and 1,000-kernel weight. The mean square values for (d) was also significant for 1,000-kernel weight. This indicated that certain forms of reciprocal differences existed for these characters. For each of the thirteen characters studied the mean square value for (a) was significant except for ear length, indicating that there was additive genetic variability amongst the parents for all characters. For flag leaf breadth, ear length and the number of spikelets per ear, neither dominance nor maternal effects were present. The remaining ten characters all showed some form of dominance. The components of genetic variation (Table 10) indicated that dominance was either complete or nearly complete for anthesis date, flag leaf length, ear length, and yield per plant. Dominance was partial for peduncle length, extrusion length, the number of kernels per ear, 1,000-kernel weight and yield per ear, and transgressive for sheath length. For anthesis date, flag leaf length, extrusion, number of ears per plant, 1,000-kernel weight and yield per ear, the significance of (b_2) together with values for $H_2/4H_1$ below 0.25 indicated that the parents carried unequal proportions of negative and positive alleles for these characters. The high positive values for F found for the anthesis date, flag leaf length, 1,000-kernel weight, yield per ear, peduncle, and extrusion indicated an excess of dominant genes.

The values of heritability calculated from the data showed that the characters, anthesis date, peduncle, extrusion, 1,000-kernel weight and yield per ear were highly heritable and that the characters,

Table 9

MEAN SQUARE VALUES FROM THE ANALYSIS OF VARIANCE FOR 5 X 5 DIALLEL TABLE
 (GREENHOUSE, 1968-69)

	a	b	b ₁	b ₂	b ₃	c	d	error
d.f.	4	10	1	4	5	4	6	24
Anthesis date	254.30**	58.60**	382.20**	33.40**	14.00**	9.90*	6.20	2.90
Flag leaf length	34.72**	17.55*	0.29	21.89*	17.51*	4.99	3.62	6.07
Flag leaf breadth	0.05	0.01	0.02	0.01	0.02	0.01	0.00	0.01
Peduncle length	45.17**	4.95*	2.87	4.61	5.66	18.27**	2.96	2.17
Extrusion length	49.28**	6.08*	7.58*	7.18*	4.89*	13.52**	2.69	1.58
Sheath length	4.10**	0.77	4.80	0.68	0.04	0.96	0.42	0.70
Ear length	0.17	0.27	0.43	0.42	0.11	0.34	0.51	0.49
Ear No. per plant	5.74**	3.67**	6.48*	3.75*	3.05*	3.50*	1.89	1.07
Spikelet No. per ear	13.13**	4.06	0.36	3.80	5.01	1.77	3.14	1.93
Kernel No. per ear	0.72**	0.32	1.06*	0.31	0.17	0.11	0.19	0.15
1,000-kernel wt.	70.90**	10.90*	2.60	14.90**	9.40*	23.40**	11.20*	3.10
Yield per ear	0.09**	0.05*	0.01	0.08*	0.03*	0.02	0.02	0.01
Yield per plant	2.06*	1.23	4.99**	0.75	0.86	1.85	0.65	0.73

** - significant at 0.1%

** - significant at 1%

* - significant at 5%

Table 10

 COMPONENTS OF GENETIC VARIATION FOR 5 X 5 DIALLEL CROSSES
 (GREENHOUSE, 1968-69)

	D	H ₁	H ₂	F	(H ₁ /D) ^{1/2}	H ₂ /4H ₁	h ²	k
Anthesis	74.75**	63.03*	54.53**	32.31	0.92	0.22	0.66	0.82
Flag leaf length	11.94*	17.27	13.62	9.81	1.20	0.19	0.35	-0.54
Flag leaf breadth	0.07	0.88	0.93	-0.66	3.65	0.26	0.20	-0.63
Peduncle length	9.84**	3.55	2.98	2.03	0.60	0.21	0.59	0.69
Extrusion length	11.82**	6.22	4.37*	4.21	0.72	0.18	0.67	0.43
Sheath length	0.36	0.73	0.50	-0.04	1.41	0.17	0.13	-0.85
Ear length	0.45	0.41	0.15	0.78	0.95	0.09	0.22	-
Ear No. per plant	0.16	3.01*	2.26*	-0.35	4.26	0.18	0.03	-0.54
Spikelet No. per ear	4.11*	4.70	2.95	3.42	1.07	0.16	0.41	-0.08
Kernel No. per ear	0.28*	0.19	0.14	0.21	0.83	0.17	0.44	0.55
1,000-kernel wt.	28.00**	11.70	8.90	17.60*	0.64	0.17	0.95	0.77
Yield per ear	0.48*	0.57	0.36	0.54*	0.85	0.16	0.63	0.75
Yield per plant	0.48	0.82	0.79	-0.76	1.27	0.24	0.18	-0.95

*** - significant at 0.1%
 ** - significant at 1%
 * - significant at 5%

flag leaf length, the number of spikelets per ear, number of kernels per ear also showed a high proportion of additive variation.

The correlation coefficient k between parental measurements (Y_r) and parental order of dominance ($W_r + V_r$) was calculated for characters considered. According to Hayman (1954b) $k = +1$ means that recessive genes must be mostly positive; $k = -1$ means that dominant genes are mostly positive; when k is small, equal proportions of dominant genes are positive and negative. For sheath length, yield per plant and anthesis date, dominance was not unidirectional. For sheath length ($k = -0.85$) dominance was controlled by excess positive genes while for the anthesis date ($k = 0.82$) dominance was controlled by excess negative genes, so that long sheath and earliness was dominant over short sheath and late flowering. For yield per plant ($k = -0.89$) dominance was in the positive direction, indicating that most of the dominant alleles in the parents were acting in the direction of high yield and recessive alleles in the direction of low yield. For flag leaf length, flag leaf breadth, peduncle, extrusion, ear number per plant, yield per ear, kernel number and 1,000-kernel weight, the values of k together with the significant values of H_1 suggested about equal proportions of positive and negative dominant genes were in control of these characters.

Field Trial in 1969

The F_1 Diallel Table

Of the thirteen characters studied the value for (c) was significant for anthesis date and peduncle (Table 11). The value for (d) was significant for anthesis date only. Thus maternal effect was

Table 11

MEAN SQUARE VALUES FROM THE ANALYSIS OF VARIANCE FOR $5 \times 5 F_1$ DIALLEL TABLES
(FIELD, 1969)

Degree of freedom	a	b	b_1	b_2	b_3	c	d	error
	4	10	1	4	5	4	6	10
Anthesis date	28.09**	9.06**	34.26**	2.94	8.93**	6.89*	11.10**	2.22
Flag leaf length	0.56	0.74	4.76	0.40	0.21	0.70	0.59	0.63
Flag leaf breadth	1.28*	0.22	0.82	0.04	0.25	0.33	0.11	0.20
Peduncle length	123.78**	3.93**	13.75**	2.42*	3.17*	2.36*	1.16	0.93
Extrusion length	96.78**	2.57	10.65**	1.76	1.61	1.43	0.60	0.93
Sheath length	5.57**	0.32	0.35	0.19	0.40	0.25	0.15	0.19
Ear length	1.88**	0.11**	0.01	0.12*	0.13*	0.01	0.01	0.01
Ear No. per plant	24.17**	6.29	20.78*	4.36	4.95	1.59	3.97	3.02
Spikelet No. per ear	6.16**	0.85	2.51	1.26	0.19	0.22	1.10	0.75
Kernel No. per ear	804.56**	37.50	70.60	49.45	21.34	66.03	37.84	38.98
1,000-kernel wt.	7.61**	4.03*	6.85*	4.30*	3.25	1.33	0.78	1.00
Yield per ear	35.12**	3.58	5.23	3.32	3.45	5.52	4.19	4.72
Yield per plant	151.86**	18.25	91.45**	2.92	15.87	5.42	8.93	7.53

*** = significant at 0.1%

** = significant at 1%

* = significant at 5%

present in the inheritance of these two characters.

For all the characters studied the mean square values for (a) were significant, indicating that there was marked additive genetic variability amongst the parents for these characters. For five of the characters (flag leaf breadth, sheath length, number of spikelets per ear, number of kernels per ear and yield per ear) there was no indication of dominance attributable to any source.

The components of genetic variation (Table 12) showed that dominance was either full or nearly full for the number of ears per plant and yield per plant. For 1,000-kernel weight there was indication of overdominance. The values of $H_2/4H_1$ for flag leaf breadth, sheath length and yield per plant were close to the maximum 0.25 indicating that the parents carried equal number of negative and positive alleles for these characters. The sign of F values also showed that an excess of dominant genes were present in the parent for the characters, peduncle length, extrusion, spikelet and kernel numbers per ear and ear numbers per plant. The calculated heritability showed that with the exception of 1,000-kernel weight all characters were highly heritable. This was to be expected from the significant value obtained for (a) in the analysis of variance.

The correlation coefficients \underline{k} between the parental values and the sum of W_r and V_r , the order of dominance, showed that broad flag leaves were completely dominant over narrow ones. For the other characters either H_1 was not significant or \underline{k} was small. This suggested that either the excess of negative or positive genes was large enough to show dominance, or that the dominance effect resulted from other sources.

Table 12
COMPONENTS OF GENETIC VARIATION FOR 5 X 5 F₁ DIALLEL CROSSES
(FIELD, 1969)

	D	H ₁	H ₂	F	(H ₁ /D) _{1/2}	H ₂ /4H ₁	h ²	k
Anthesis date	16.12**	18.46*	17.03*	6.52	1.07	0.23	0.55	
Flag leaf length	-0.60	-0.21	0.01	-0.72	-	-	-	-
Flag leaf breadth	0.51**	0.43*	0.41*	0.02	-	0.91	0.24	0.53
Peduncle length	52.50**	6.89	5.98	4.25	0.36	0.22	0.92	-0.68
Extrusion length	43.60**	3.78	3.29	5.75	0.29	0.22	0.99	-0.69
Sheath length	2.01**	0.37	0.34	-0.13	0.43	0.23	0.70	0.68
Ear length	1.03**	0.10	0.08	0.34*	0.32	0.18	1.06	0.55
Ear number per plant	10.72**	10.73*	9.15	3.32*	1.00	0.21	0.48	0.002
Spikelet number per pear	4.95**	1.97*	1.32*	3.21*	0.63	0.17	0.99	-0.15
Kernel number per ear	77.32*	26.01*	19.36*	6.78	0.58	0.19	0.78	-0.25
1,000-kernel wt.	2.43	7.92	5.97	1.76	1.81	0.19	0.22	-0.93
Yield per ear	9.59**	8.80	6.88	-2.49	0.96	0.20	0.45	0.29
Yield per plant	57.71**	28.64*	29.11**	-2.02	0.70	0.25	0.59	-0.32

*** - significant at 0.1%

** - significant at 1%

* - significant at 5%

The F_2 Diallel Table

The analysis of variance for diallel table constructed from F_2 generation data gave significant values for (a) for all characters (Table 13); thus showing the importance of additive gene action. The only other indication of significant differences were reciprocal differences for peduncle length. In this generation dominance was not significant for any of the characters studied. The heritability, as expected, was high for all of them.

Non-allelic Interaction

The regression coefficients of W_r on V_r for all the characters in F_2 , backcross of the 1969 plant, and F_1 of both 1968 and 1969 plantings were presented in Table 14, together with the joint regression coefficients for F_2 and backcross in 1969. Only the joint regression coefficient for kernel number was significantly different from unity.

The χ^2 values in the last column of Table 14 were calculated from the $(2L_2 - L_1)$ diallel table as suggested by Hayman (1957), for a test of the significance of general existence of non-allelic interaction. L_2 was the F_2 family mean value and L_1 was the F_1 family mean value. From the $(2L_2 - L_1)$ diallel table, χ^2 was calculated for each character and was tested with $1/2n(n-1)=10$ degrees of freedom. Since none of these χ^2 values were significantly different from zero, there was no evidence of a non-allelic interaction. This result also confirms the validity of the hypotheses on which this diallel analysis was based.

Genotype-environmental Interaction

The combined analysis of the first two replications of the

Table 13

MEAN SQUARE VALUES FROM THE ANALYSIS OF VARIANCE FOR $5 \times 5 F_2$ DIALLEL TABLES
(FIELD, 1969)

Degree of freedom	a	b	b_1	b_2	b_3	c	d	Error	Heritability
	4	10	1	4	5	4	6	10	
Anthesis date	19.05**	1.28	0.51	0.84	1.78	1.64	2.45	2.13	0.78
Flag leaf length	0.22	1.03	3.53	0.52	0.93	1.38	0.75	1.00	-
Flag leaf breadth	2.37**	0.47	0.12	0.81	0.26	0.27	0.29	0.28	0.75
Peduncle length	90.37**	0.87	0.26	0.39	1.38	15.42	10.16	1.21	0.84
Extrusion length	65.53**	0.85	0.29	0.37	1.35	8.94	6.48	7.46	0.72
Sheath length	8.04**	0.14	0.01	0.23	0.10	0.96	0.67	0.78	0.52
Ear length	2.52**	0.14	0.01	0.07	0.22	0.21	0.14	0.17	0.72
Ear No. per plant	39.49**	1.87	0.37	1.82	2.22	0.61	2.85	1.96	0.76
Spikelet No. per ear	7.13**	0.22	0.07	0.16	0.29	2.05	2.65	2.41	0.77
Kernel No. per ear	547.59**	19.06	50.48	23.79	8.98	47.45	74.59	48.91	0.67
1,000-kernel wt.	14.27**	2.45	5.04	3.31	1.32	4.38	0.73	2.19	0.66
Yield per ear	18.49**	1.47	4.70	2.03	0.38	2.67	2.71	2.69	0.32
Yield per plant	110.14**	8.61	11.16	14.52	3.37	9.22	2.49	5.19	0.46

** - significant at 0.1%

** - significant at 1%

* - significant at 5%

Table 14

REGRESSION COEFFICIENTS OF W_Y ON V_Y FOR 5×5 DIALLEL TABLES
 IN F_1, F_2 AND BACKCROSS GENERATIONS

	$F_1, 1968$	$F_1, 1969$	$F_2, 1969$	$BC, 1969$	Joint $BC \& F_2$	χ^2
Anthesis date	0.729 ± 0.148	0.921 ± 0.349	1.329 ± 0.434	1.176 ± 0.165	1.203 ± 0.113	3.76
Flag leaf length	0.498 ± 0.473	0.534 ± 0.277	0.596 ± 0.263	1.147 ± 0.496	0.928 ± 0.301	12.85
Flag leaf breadth	0.952 ± 0.446	0.710 ± 0.237	0.902 ± 0.342	0.254 ± 0.342	0.181 ± 0.204	4.22
Peduncle length	1.139 ± 0.161	0.927 ± 0.275	0.948 ± 0.027	0.997 ± 0.035	0.996 ± 0.200	0.97
Extrusion length	1.197 ± 0.207	0.992 ± 0.237	0.995 ± 0.039	1.036 ± 0.070	1.007 ± 0.064	1.07
Sheath length	0.856 ± 0.205	0.950 ± 0.364	1.219 ± 0.140	1.218 ± 0.140	1.273 ± 0.152	0.88
Ear length	1.036 ± 0.188	0.996 ± 0.126	0.915 ± 0.129	1.180 ± 0.128	1.199 ± 0.110	1.53
Ear No. per plant	0.623 ± 0.355	1.191 ± 0.437	0.878 ± 0.122	1.120 ± 0.220	1.089 ± 0.114	9.00
Spikelet No. per ear	0.511 ± 0.288	0.883 ± 0.232	1.260 ± 0.125	0.969 ± 0.146	1.005 ± 0.085	0.55
Kernel No. per ear	1.059 ± 0.576	0.998 ± 0.128	0.967 ± 0.044	0.447 ± 0.130	0.634 ± 0.373	1.40
1,000-kernel wt.	1.486 ± 0.256	0.437 ± 0.303	0.296 ± 0.248	0.702 ± 0.078	0.642 ± 0.177	2.78
Yield per ear	1.017 ± 0.765	0.668 ± 0.208	0.973 ± 0.008	0.416 ± 0.207	0.662 ± 0.230	1.75
Yield per plant	0.467 ± 0.336	0.916 ± 0.046	0.812 ± 0.122	0.790 ± 0.104	0.815 ± 0.069	3.37

field experiment for yield and its components and the parental performances in the greenhouse was presented in Table 15. Environmental and parental differences were significant. The varietal differences for kernel number per ear was not significant but the error was large. A variety-environmental interaction was also present for both yield and its components.

The significant genotype-environmental interaction represented a departure from the hypothetical genetical model on which the diallel analysis was based. This suggested that the results of the diallel analysis had been distorted by this interaction. However, it was still reasonable to state that the result of diallel analysis was applicable in the environment from which the data was collected because no combined analysis over two growth conditions was attempted.

Table 15

MEAN SQUARE VALUES FROM THE COMBINED ANALYSIS OF PARENTAL PERFORMANCE
OVER TWO ENVIRONMENTAL CONDITIONS

Source of variation	Mean Square				Degree of freedom
	Yield per plant	Ear No. per plant	Kernel No. per ear	1,000 kernel weight	
Block	0.1	2.6	0.1	0.01	1
Environment	1435.8***	570.3***	236.9***	334.5***	1
Variety	43.2***	8.0***	73.2	17.5***	4
Variety x environment	48.4***	8.8***	86.8*	60.5***	4
Error	2.1	1.4	22.2	2.0	9

*** - significant at 0.1%

** - significant at 1%

* - significant at 5%

CHAPTER V

DISCUSSIONS

Relationships Between Yield, Yield Components, and Structures above the Flag Leaf Node

The simple correlation coefficients between yield per plant and ear numbers per plant, kernel numbers per ear and 1,000-kernel weight were consistent for the trials in the greenhouse (Table 1) and in the field (Table 5). That the correlation between yield per plant and 1,000-kernel weight was not significant in the field trial was probably due to the sampling error. Other workers have reported similar results for the correlations between yield and its components, (Krishnamurthy, 1968; Fonseca and Patterson, 1968; Tha and Ram, 1968; Malik et al, 1968; Johnson et al, 1968; Smocek, 1969; Lebsack and Amaya, 1969; Jain et al, 1969; Reddi et al, 1969).

For yield components, a negative correlation was found between kernel numbers per ear and 1,000-kernel weight in the greenhouse, and between 1,000-kernel weight and ear numbers per plant in the field. Similar results and observations were reported by Fonseca and Patterson (1968), and Johnson et al (1966). As long as the product relationship between yield and its components exists and since plant varieties may have the same yield but achieve it in different ways, then negative correlations among the components are to be expected. However, this relationship can not be consistent and varies with the environmental conditions, the plant types used, and also with the genotype-environmental interaction.

Since yield components are determined at different times, they are differentially affected by variation in environment (Thorne et al,

1968). In this study, no attempt was made to explore this aspect. However, significant environmental differences and genotype-environmental interactions were found for yield and its components (Table 15). This suggests that the genotype-environmental interaction might be the reasons why the correlation between yield components was not consistent in two environments.

In this study, ear numbers per plant was found to make the largest contribution to yield (Table 2 and Table 6). This agreed to the findings of Jain et al (1969), Austenson and Walton (1970), and Fonseca and Patterson (1968). However, different results were also reported by Krishnamurthy (1968), and Tha and Ram (1968). These discrepancies in the relative importance of yield components may be explained by plant type characteristics. Reddi et al (1969) in a cross of Norin 10 with other two varieties found that lines with shorter culm tended to have longer ear and lower kernel weight and that these were the characteristics of the Norin 10 donor parent. More generally, in a principal component analysis, Morishima et al (1967a and b) identified a "panicle-number" type and a "panicle-length" type in rice. If, following the same approach, wheat varieties were classified into "ear-number" type and "ear-weight" or "ear-length" types, different "weight" should be given to yield components for different varieties. In the combined analysis of parental performances over two environments, it was observed that in favourable field conditions, Manitou, Pitic 62 and Wisconsin 261 gave substantial increases in yield associated with large increases in ear numbers, while Inia 66 and Lerma Rojo 64A gave high increases in 1,000-kernel weight (Table 16). For these reasons, Manitou, Pitic 62 and Wisconsin 261 may be classified as "ear-number" type and

Table 16
MEAN MEASUREMENTS OF YIELD AND YIELD COMPONENTS FOR PARENTAL VARIETIES IN TWO ENVIRONMENTAL CONDITIONS

Variety No.	Yield per plant		Ear No. per plant		Kernels per ear		1,000-kernel weight Green- house
	Green- house	Field	Green- house	Field	Green- house	Field	
1. Manitou	2.97	19.25	5.75	14.55	23.50	24.34	28.19
2. Pitic 62	2.50	32.15	3.25	19.31	28.30	45.99	37.38
3. Lerma Rojo 64A	1.99	17.35	3.75	10.94	25.00	41.10	26.51
4. Inia 66	2.42	12.88	4.00	10.56	37.50	28.85	22.59
5. Wisconsin	3.15	16.53	5.00	14.27	27.30	32.82	29.89
The error for variety comparisons	0.53	0.35	0.55	0.50	0.55	0.50	0.50
The error for environment comparisons	1.05	0.70	1.1	1.0	1.1	1.0	1.0

Inia 66 and Lerma Rojo 64A as "intermediate" type. Ear number was important in determining the yield of both types in these aspects, a conclusion which agreed with the partial regression analysis results.

Therefore the relative importance of yield components depends upon the type of varieties used for analysis. In addition, because of the genotype-environmental interaction, there are important differences in the way in which yield is built up from its components under different growth conditions. In the present study, the highest yielding variety in the field, Pitic 62 (Table 16), was the third highest yielding variety in the greenhouse although it had the highest 1,000-kernel weight. The principal yield component that made up its high yield in the field was ear number followed by kernel number per ear. This fluctuation in yield components is evidently a result of genotype-environmental interaction.

The morphological characters, when related to yield and yield components (Table 2 and Table 6), showed that higher levels of significance were obtained for the partial correlation coefficients in the greenhouse than in the field. There were two possible explanations. First, environmental variations might be smaller under the more uniform condition prevailing in the greenhouse. Second, inspite of supplementary lighting, the light intensity was likely to be lower in the greenhouse in winter than during the summer in the field. Consequently, the extent of the photosynthetic area would be of greater importance in relation to yield under greenhouse conditions. This difference in light intensity and photoperiod would also explain the differences found between the two types of planting conditions. A paired t-test indicated that the date of anthesis and the flag leaf sheath length did not differ

significantly in these two conditions while ear length, peduncle length and extrusion length were greater in the field. The number of spikelets per ear, flag leaf length and breadth were all significantly greater in the greenhouse. As reported by Friend (1966) extending a daylength from 8 hours to a longer photoperiod by low-intensity radiation resulted in a longer leaf lamina. The same author (1966) also found that ear length was increased with increased light intensity and temperature, and long ears with many spikelets were formed at low temperatures. These findings might explain why ears were longer in the field and had more spikelets in the greenhouse.

Apart from these differences there was a fair degree of agreement between the results from the two growth conditions. In both cases sheath length and flag leaf breadth were associated with yield per plant and its components. The effect of flag leaf breadth on yield per plant confirmed the observation by Tanner et al (1966) who emphasized the importance of both flag leaf breadth and leaf angle in categorizing high yielding strains in wheat, barley and oat nurseries and suggested that these two leaf characters would provide a useful criterion in selection for yield.

Sheath length was consistently associated with yield per plant and ear numbers, but its relations to yield per ear and spikelet number in the greenhouse was not found in the field trial. In greenhouse condition, Simpson (1968) also found that sheath area was associated with yield for 120 varieties.

In determining leaf area, both leaf length and leaf breadth are important. Smocek (1969) found that the area of the youngest leaf

was associated with the kernel numbers per ear and average weight of one grain. In this study the flag leaf length was closely associated with both kernel number in the greenhouse and kernel weight in the field, while flag leaf breadth was associated with kernel number in the field. Other evidence supporting the association between flag leaf area and yield were reported by Walton (1969) and Simpson (1968).

Longer ears usually provide sites for more spikelets and thereby allow for an increased kernel number. Therefore, the close association between ear length and spikelet and kernel number was to be expected. The length of extrusion showed negative association with kernel numbers in the field trial, indirectly it affected the yield per plant and yield per ear. This negative relationship did not agree with the positive relation found by Walton (1969).

Generally, the results of factor analysis from both greenhouse and field trials supported the conclusions drawn by partial correlation and regression analysis. Furthermore, since there were high multiple correlations between yield and yield components, and morphological characters, it could be concluded that a combination of ear length, sheath length, ear number and spikelet number contributed about 28% to the yield per plant. Kernel number, extrusion and flag leaf breadth accounted for 15-27%, and 1,000-kernel weight and flag leaf length accounted for 15-20% of the yield.

By means of stepwise multiple regression method, it was found that when yield per plant was predicted by yield components and morphological characters, yield components accounted for most of the total yield variation. Morphological characters played only a minor part. This implied that the effects of morphological characters on yield per

plant were indirect, i.e. through their effects on yield components. Thus, longer ear provides sites for more spikelets and thereby increases kernel number. Increasing flag leaf length would effect the source by increasing leaf area, and the sink by increasing kernel weight. This indicated that kernel size was partly determined during the vegetative growth, but was largely a function of the post-fertilization stage (Thorne, 1966). The relation between flag leaf breadth and kernel number probably could be explained by the large photosynthetic area which provided the nutrition for fertilization and meiosis.

Following the plant type approach and confining consideration to morphological parts above the flag leaf node, the evidence obtained from these trials suggested that a wheat plant with moderate short but broad flag leaf, long flag leaf sheath, short extrusion, long ear and moderate high tillering capacity would be desirable for increasing yield per plant. In considering the shape of leaves, Jennings and Beachell (1967) pointed out that, short, relatively narrow, thick, erect, dark-green leaves that remain functional until shortly before harvest were closely associated with nitrogen responsiveness. Furthermore, width of leaves did not seem to be as critical as length, although moderate width might be preferred over relatively wide leaves. They also stated that this did not apply to the flag leaf. A rather broad flag leaf that was short and predominantly erect, was desirable rather than one that was long and narrow. The results of these studies also supported the observation of Tanner et al (1966). However, in barley, Fowler and Rasmusson (1969) observed that the leaf area of adjacent leaves was highly correlated. Thus it is difficult to develop plants that have individual leaves of distinctly different size. One of the

varieties, Pitic 62, which was short-statured, with a long sheath and short extrusion, a long ear and was moderately high tillering, accompanied by broad and moderately long flag leaves was also the highest yielding parent.

Inheritance of Yield, Yield Components, and Morphological Characters above the Flag Leaf Node

Evidence from the present study showed that yield per plant and its components were controlled by polygenes and were closely associated with additive gene actions. Dominance played some part, but not an important one. In the F_1 generation, dominance was more important in the greenhouse than in the field, and was not significant in F_2 generation. This was to be expected because the dominance present in the second generation would be half of that shown in the first generation. Not only would the magnitude of dominance be smaller in the second generation but there would be more bias involved in the estimation, because the error term contained not only environmental variation but sampling error in the segregating generation.

In so far as additive genetic variation was concerned, the conclusion concerning the inheritance of yield and its components agreed with the findings by Whitehouse et al (1958), Lupton (1961), Krousted and Foote (1964), Williams (1967), Brown et al (1966) and Gyawali et al (1968). There was not, however, full agreement with other workers about the importance of dominance.

For yield per plant, Anwar and Chowdhry (1969) also found overdominance. The absence of non-allelic interaction in this study did not agree with Whitehouse et al (1958), Lupton (1961) and Williams (1967), though Chapman (1967) also found that yield was conditioned by genes

with dominance effects. Here dominance for ear number, was complete while little dominance was observed by Whitehouse et al (1958), Krousted and Foote (1964) and Chapman (1967). Lupton (1961) found recessive genes to be responsible for high values in ear number. The importance of additive, dominance and epistatic effects for this character were also reported by Williams (1967). In contrast with the partial dominance found here for kernel number, complete dominance was observed by Lupton (1961), the presence of additive-dominance epistatic effects were also reported by Williams (1967). The conclusion that 1,000-kernel weight was controlled by additive gene action did not agree with Chapman (1967) who found that dominance was more important. Krousted and Foote (1964) also found no significant general combining ability for this character. However, Whitehouse et al (1958), Lupton (1961) and Brown et al (1966) observed little dominance. The partial dominance found in the greenhouse trial agreed with Williams (1967). That the inheritance of spikelet numbers per ear was controlled simply by additive gene action agreed fairly well with Whitehouse et al (1958).

The differences between these results and those of earlier workers might be explained by the action of different groups of genes in different environmental conditions (Whitehouse et al, 1958), and in different sowing methods between spaced and drilled (Lupton, 1961). Moreover, the use of different varieties could also have resulted in a different specific combining ability.

In the present study, the additive gene action for yield and its components was consistent over growth condition and generations, suggesting that additive gene action was not susceptible to environmental effects. On the other hand, dominant gene action, greatly affected by

environmental factors, was shown in the two different environments. Not only the presence of dominance, but also the degree of dominance was subject to environmental influence. Similar results were observed in corn by Rojas and Sprague (1952), Matzinger et al (1959) and Lonngquist and Gardner (1961). Thus, in estimating dominant gene action, hybrids should be grown in different locations for several years so that a more precise result can be obtained.

Although the lack of a general dominance effect for yield and its components in F_1 generation and for all of them in F_2 generation in the field were indicated by the lack of significance for (b) in the analysis of variance, heterosis was revealed by the significance of (b_1) for yield per plant under both growth conditions. In view of reports by Briggle (1963), and Johnson and Schmidt (1968), it was not surprising this occurred in a self-pollinated crop. However, it was interesting to note that in the greenhouse, heterosis was associated with moderate overdominance for yield per plant, and was accompanied by heterotic ear number with overdominance and heterotic kernel number with partial dominance. In the field trial, heterosis for yield per plant was associated with partial dominance and was accompanied by heterotic ear number with complete dominance and heterotic 1,000-kernel weight with moderate overdominance. This indicated that heterosis for yield was due to the favorable interaction of the yield components, and suggested that heterosis was associated with overdominance and other degrees of dominance. This result agreed with the views indicated by Allard (1960), and Briggs and Knowles (1967).

The heritabilities estimated for yield and its components were generally high indicating that a major part of the total phenotypic

variability for these characters were genetical. These estimates were not consistent in two environmental conditions. The decrease in dominance in the second generation was also accompanied by an increase in heritability. Similar results were reported by Krousted and Foote (1964), Johnson et al (1966), and Fonseca and Patterson (1968). The differences among those estimated may be explained by the reasons given by Hanson (1963) who considered that heritability estimates were influenced by the method of estimation, the generation of the hybrid, the experimental sample basis, and the environment.

Generally, anthesis date was a character controlled by polygenes which showed both additive and complete dominance effect. An excess of dominance genes with negative effects indicated dominance for earliness. In the range of materials studied the correlation between anthesis date and heading date was high ($r = 0.953$). It was therefore not surprising that conclusions reached here agreed well with the results obtained by Crumpacker and Allard (1961). Similarly, Chapman (1967) found that heading date was conditioned by additive and dominance effects. Anwar and Chowdhry (1969), using Pitic 62 and three other spring wheat varieties, also found that earliness of heading was controlled by additive genes with partial dominance. The heritabilities estimated were higher than the ones obtained by Johnson et al (1966) and similar to those of Crumpacker and Allard (1962), and Fonseca and Patterson (1968). These high heritabilities ensure a marked response in selecting for earliness.

Similar to the inheritance of yield and its components, morphological characters above the flag leaf node were also controlled by

genes having significant additive action with various degrees of dominance effects. Except for flag leaf length, all of the other morphological characters studied showed consistent additive gene action over two different growth conditions. However, the presence and degree of dominance was different. The dominance effects were all insignificant in F_2 generation in the field. The additive and dominance gene action for ear length agreed fairly well with Walton's (1969), results but not with Johnson et al (1966), who found that completely additive gene actions were in command. Sheath length was primarily additive although some overdominance and heterosis for long sheath was indicated in the greenhouse trial. The partial dominance for short extrusion did not agree with the overdominance obtained by Walton (1969), but the additive gene action did.

The peduncle essentially a sum of extrusion and sheath, was inherited in a different way. In the F_1 generation, additive, dominance and maternal effects were all important in the two growth conditions. In F_2 generation, however, only additive and maternal effects remained significant. Heterosis in the negative direction and asymmetry of gene distribution were the main part of the dominant gene action.

Conclusion

In this study, the morphological characters above the flag leaf node, as well as the components of yield, were shown to be closely associated with the grain yield in wheat. Furthermore, the effects of morphological characters on yield were found to be indirect, through their effects on yield components. The length of ear and sheath, and the flag leaf breadth were the more important morphological characters

studied, and their effects were mainly in increasing the number and size of kernels.

The agronomic and morphological characters under study were primarily controlled by genes having additive effects. Herabilities for the length of ear, extrusion, sheath and peduncle were very high indicating that they were mainly controlled by additive genes as was the flag leaf breadth and the components of yield. Flag leaf length, in the greenhouse, was controlled by both additive and dominance gene action. Some overdominance was also indicated. A lower degree of dominance implies that early generation selection will be more effective, while a high degree of dominance suggests later generation selection.

From this information, it is evident that increasing grain yield by selecting for structures above the flag leaf node is a promising approach. However, the importance of the yield components cannot be ignored. King et al (1967) showed that photosynthesis by the flag leaf was directly regulated by the demand for photosynthate, and they concluded that while there were occasions when rate of photosynthesis limited crop yield, there might also be situations where demand for photosynthate limited crop yield. Hence both source-photosynthetic area and sink-yield components are important. The findings of Smocek (1968) also supported this view.

In a breeding program, selection of the parents is an important step. The use of diallel cross analysis would provide valuable information for understanding the genetic merit of the parents. Since the five parents used in these studies were not randomly chosen and the range of materials was not very large, the information obtained here

might not have general application. In order to avoid the large error introduced in the F_2 generation analysis, larger population should be used.

In solving the multivariate dependence structure, factor analysis which, used in the present study, appeared to be a very good method.

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